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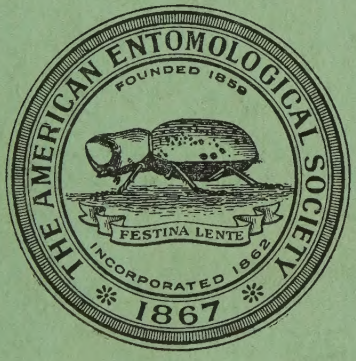

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THE EVOLUTION AND DISTRIBUTION OF AMERICAN BUMBLEBEE KINDS

BY HENRY J. FRANKLIN

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This paper is intended to present some of the material, at least in fragmentary form, which has been accumulating in the hands of the author during his 43 years service in the cranberry industry, as attention to that service has made it impossible to develop the bumblebee study thoroughly. The conditions of age and health in which the author finds himself in assuming responsibilities for this study will necessarily cause the material to be presented in a very different condition of quality and arrangement than it would have been had this attempt been made under more favorable circumstances.

While this study of the effects of changes of climate and of geology on the bumblebees is devoted mostly to the American species, it also touches widely, though briefly, on some of those of other parts of the world. The species grouping followed is basically that first developed by Radoszkowski (Bul. Soc. Natural Moscow. XLIX, 1884) but much modified by the work of others—See List of References on page 51. In some respects this grouping is not very good science for the use of sectional names so followed can hardly be defended except on grounds of convenience, as they have no recognized status in nomenclature. Their use here, however, appears to have the advantage of helping to clarify certain evolutionary developments:

1. *The Influence of the Great North.*—This appears mostly in important male characters common to the subgenera recognized as comprising the North American portion of the section *Anodontobombus*: namely, *Alpinobombus, Terrestribombus,* and *Pratobombus.* The noteworthy characteristics here should be regarded as parallel or convergent developments in the three essentially unrelated subgenera (as shown clearly by the differences in the heads of the sagittae) mentioned. They are: (a) Hind tibiae with more

or less considerable corbiculae; (b) Claspers, especially the volsellae, considerably reduced, suggesting a weak clasping function; (c) Flagellum of antenna of males short to average;[1] (d) Relative earliness of the life-cycle in the active season. These evolutionary developments may be regarded as having been induced by conditions of the far North, probably mostly those of climate, for they now appear in all the many species making up the subgenera concerned. The character of these species and subgenera (variation) suggest that they still are in a condition of active analogous evolution and all together they suggest modern development. If we regard the cooling of the North as a basic creative element here, we can probably believe that the developments under notice had their beginnings in early Pliocene time and have so far continued perhaps hardly more than a million years.

2. *The Influence of the Rise of Great Mountain Systems and Dry Plateaus.*—The bumblebees of the *Boopobombus* section, introduced by Frison (1927, Amer. Ent. Soc. Trans. 53:62) are found mostly in connection with such developments of the earth in its various regions overall except in some where the bumblebees are entirely or mostly absent.

The subgenera included here are rather many but mostly few in species,[2] in striking contrast with those of *Anodontobombus*. In *Boopobombus*, as in *Anodontobombus*, the leading matter of interest here is the parallel or convergent development of characters in more or less unrelated groups or species. We must now draw attention to peculiar characters of the males of the species of *Boopobombus*. To bring this out most clearly, it seems a likely procedure to discuss these characters in order, one by one, and point out where they seem to fit in the argument. The males of

[1] This north-south antennal relation is also true in *Psithyrus* the world over. *P. vestalis* and *P. distinctus* are especially interesting here.

[2] This is believed to be very significant and to be expected of species of very old distributions that adjusted themselves to a mountain habitat possibly hundreds of thousands of years ago. Species like *Bombus huntii* Greene and *Bombus occidentalis* Greene evidently are in a very different category, being of relatively quite recent mountain distributions. There seem to have been at least three widespread mountain distributions of bumblebees in western North America, separated by immensely long intervals of time and represented in order now mainly by (1) *Bombias* Robertson and *Fraternobombus* Skorikov, (2) *Separatobombus* Frison and *Crotchiibombus* (p. 50), and (3) *Bombus* Latreille, *Pratobombus* Vogt, *Subterraneobombus* Vogt, and *Rufocinctobombus* Frison. The latter of the two separating intervals probably was much longer than the former, judging by comparative anatomy of the species concerned.

all these species have large eyes, these being of varying size as between the different subgenera, and the ocelli also having increased size. The length of the flagellum of the antennae as related to that of the scape is generally reduced more or less as compared with that of many other bumblebees. This evolution appears to be due partly to the reduction in the density of the air and in its water content (absolute humidity), in which these bumblebees live. The more the flagellum of the antennae is reduced in length, the greater is the tendency to the development of large eyes and ocelli, the probable reduction in the effective sense of smell evidently being compensated for by the improved facilities for sight.[3] Related to this is the considerable amount of modification in the venation of the wings, which no doubt has come about through the influence of the rarification of the atmosphere in high regions. Presumably the development of these characters of the males of *Boopobombus* has taken place as a result of the rise of the mountain systems as this has been in effect in various parts of the world. It has been greatest in North America, somewhat less in Europe, and still less notable in South America and Asia. The various degrees of this development agree reasonably well with the lengths of time since the mountain systems in these different parts of the world are believed to have had their growth. As the outstanding development of the *Boopobombus* characters is found in the species *Bombus auricomus* (Robertson), *B. nevadensis* Cresson and *B. fraternus* (F. Sm.) in North America, it seems that this evolution had its beginnings in North America long before it appeared elsewhere, this undoubtedly being due to the relatively early birth in North America of great mountain systems such as the Rockies. On the other hand, these developments have been less striking in Asia, no doubt because of the more recent rise of the lofty mountain chains of that continent. We may, therefore, perhaps venture a little to guess at the times when the *Boopobombus* developments began to take place in different parts of the world. It is quite conceivable that it saw its beginnings as early as early Miocene time in western North America, whereas it is sure not to have shown any such development in Asia before late Miocene. Very prob-

[3] The relative length and importance of the third and fifth segments of the male antenna also may be interesting here. In most bumblebee males, the fifth segment is longer than the third, but in *Boopobombus* and the subgenus *Terrestribombus* the third segment is as long as or longer than the fifth.

ably the first development of *Confusibombus* of Central Europe was contemporaneous with that of *Separatobombus* in North America, this probably being Miocene. We badly need more information about the geographical distribution of *Rufocinctobombus* (Proc. of the Ent. Soc. of Washington, vol. 49, 1947, no. 6, p. 170). Judging by its relative abundance in Prince Edward Island and in collections from the Province of Quebec and Northern Alaska, it may be about the most important species of bumblebee in Canada. Its great variability in coloration throughout its wide range suggests that it is relatively a newcomer in the New World, and it seems not improbable that it had its origin in Asia and in Plio-Pleistocene times (as indicated by the size of the eyes of the males). Also the relatively small eyes of the males of some of the South American species of *Boopobombus* probably is related to the comparatively recent rise of the Andes.

Apparently related to the peculiar development in the venation of the wings in *Boopobombus* are the active habits of flight in that group noted by various observers, their peculiar character suggesting reliance on sight rather than smell for guidance.[4] Other peculiarities in the structure of these bees besides that of the venation of the wings also may be attributed to the methods of flight adopted by them in response to the character of the medium they have to maneuver in. The size of the thorax has evidently evolved as an accommodation to the great muscles which have been developed to drive the wings under the conditions mentioned. As a compensation for this great development of the thorax, there has come about in most species a more or less marked reduction in the size and, no doubt, the weight of the abdomen, this tending to reduce under difficulties arising from an increase in weight of other parts of the body.

Different groups, subgenera, of the *Boopobombus* bees seem to cling an amazingly long time to the regions they are in, especially when it is remembered that these habitats mean a present embrace of them for probably over a million years more than those had by other bumblebees. Outstanding examples of this are *Bombus confusus* Schenck of Central Europe and *Bombus morrisoni* Cress. of America. Any tendency on the part of these bees to depart

[4] See F. W. L. Sladen, The Humble-Bee, page 14, 1912; and Theodore H. Frison, 1917, Notes on Bombidae, Annals Ent. Soc. of Am., vol. x, p. 285.

from their present mountain ranges appears to be subject to a strong and lasting brake. It would appear that with these bumblebees, after the evolution of their mountain characters, there must come into play as a brake to spreading to different regions and conditions the law of the irreversibility of evolution (see Osborne, H. F., The Age of Mammals, page 34, and Julian Huxley, Evolution: the modern synthesis, pp. 497-503).

In many respects, the male honeybee has gone through an evolution in structure analogous to that of the males of *Boopobombus,* as evidenced by its immense eyes, large ocelli, and thorax fitted to hold a powerful musculature. This may fairly be taken as clear evidence that the honeybee had its origin in regions of mountains or high plateaus.

Classification of Bumblebee Kinds

One objective of this paper is to propose bases for a new system of bumblebee classification, this being advanced at present for study, rather than for acceptance.

It seems that most of the bumblebees of the New World may be placed in the following four or five groups of subgenera: 1. When we examine the sagittae of most of the forms that are now, or were formerly, basically of the North, such as those of *Pratobombus* Vogt, and much of *Boopobombus,* we find the heads are long and rather sickle-shaped and directed ventrad and *mesad* (locking device?). We may deduce from this that old close relations have existed between *Pratobombus* and much of *Boopobombus.* The subgenus name *Uncobombus* has been given to include some of these bees and others (Krüger, 1920, p. 461). The males tend to have the antennae (especially the flagellum) shortened.

Judging partly by the presence in Europe of such apparently related stand-off forms as *Bombus soröensis* Fabr., *B. lapidarius* L., and *B. mastrucatus* (Gerst.), *Pratobombus* probably had its origin in the far north of the Old World.

2. On the other hand, most of the species of bumblebees basically of the South have sagittae with heads that are short, rounded, or shell-like and directed *laterad* (subgenera: *Subterraneobombus, Fervidobombus,* and Central and South American subgenera yet to be described). The European subgenera *Agrobombus* and *Pomo-*

bombus also would belong here. The sectional name *Odontobombus,* given by Krüger, covers these bees. The males have long antennae (especially the flagellum) and mostly powerful claspers.

Some species of *Odontobombus* other than those now in the United States, being basically southern, probably were eliminated by the unfavorable conditions of the ice age. *Bombus americanorum* Fabr. probably is a newcomer from Mexico. We are reminded here of the Mexican Cotton Boll Weevil and the Mexican Bean Beetle, invaders of historic times.

No certainly basically southern species of American bumblebee, with its characteristic long male antennae, seems ever to have developed *Boopobombus* characters. This may hint that shortening of these antennae by northern racial habitation is almost a prerequisite of *Boopobombus.*

When we approach the problem of a natural classification of the bumblebees in this way we find that, besides the large groups already mentioned, there are still other forms that must be placed. The following of these should be noticed particularly. 3. The heads of the sagittae of the subgenus *Bombias* are very long and nearly straight. This is surely a very old group of the North, for it shows the extreme *Boopobombus* development. It probably was beginning to develop its *Boopobombus* character, possibly flanked on the east by the ancestral *Fraternobombus,* in the Rockies while most of the *Uncobombi* (above) were still in the far North. The ancestral forms of the latter (like *Separatobombus*) must have had strong claspers and so took to the high lands with the effect of the influence of the cold North showing but little on them. 4. *Bombus* (also called *Terrestribombus* by Vogt) is evidently very much of an isolated subgenus with a probably significant evolution. Judging by its wider distribution in the old world than in the new, it had its origin there. The sagittae are very characteristic, apparently showing little relationship to those of the other subgenera listed here. Other items tending to indicate the considerable, if not, complete, independence of this group are: (a). Outer spatha (males) remarkably wide as compared with its length. (b). Inner spatha with fenestrae, and otherwise characteristic. (c). Mandibles of females four-toothed. (d). Sting-sheath (females) two-toothed on each side, a rather unique arrangement among bumblebees. (e). Its habit, to which most other

bumblebees are not addicted, of biting into the sides of flowers is noteworthy here as is also that of having its larvae exposed in the nest and that of building large waxen tubes for the storage of pollen.

Lesson from Boopobombus

There has been much discussion [5] as to whether *Psithyrus* is monophyletic or polyphyletic, with the weight of opinion seeming to lie toward the latter view. A careful study has shown that the *Boopobombus* character has evolved at least ten separate times among the bumblebees in different parts of the world, and this seems very clear evidence that among such bees the influence of habitat has rather surprising power to bring about parallel and convergent evolutions. This is so striking that it comes near to proving that the Bombini in general have been mainly polyphyletic in their group developments. Why argue more about *Psithyrus?*

We greatly need a more extensive and intimate knowledge of the life histories and habits of the different species of bumblebees to study the probabilities of the history of their evolution and distribution effectively. Let us consider here some interesting items presented by species having wide distributions in New England: 1. *Bombus vagans* F. Sm. shows by the relatively late adjustment of its life cycle to the active season that it has been distributed rather far south in the eastern part of the country for quite a long time. That it does not range through the more southern states and is not represented there clearly may be a result of the ice age which presumably eliminated some southern species. Meanwhile, a form probably somewhat related to *Bombus vagans* F. Sm. developed, as *pre-separatus*, its *Boopobombus* character on the Great Plains. 2. *Bombus Pratobombus bimaculatus* Cress., a northern form as shown by the earliness of the adjustment of its life-cycle, now ranges throughout our eastern states. Its extensive presence clear to the Gulf of Mexico may be a result of the ice age. 3. Judging by the reddish coloration on the abdomen, *Bombus ternarius* Say had its origin in the mountainous west. It probably is rather closely related to *Bombus huntii* Greene.

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[5] Richards, O. W., Trans. Ent. Soc. Lond. LXXV, pp. 259 to 262. Frison, T. H., Trans. Amer. Ent. Soc., LIII, 1927, p. 73.

Corbicular Fringes

The corbiculae, so important in the structure of all female bumblebees as receptacles for pollen, are made up largely of fringes of long hairs placed along the front and hind margins of the outer faces of the hind tibiae. It seems that with some species it is important in the bee economy that the males should also have corbiculae, this being apparently true of the following subgenera: *Alpinobombus, Terrestribombus*, and *Pratobombus* of the North and of *Bombus dahlbomii* Guer. and *Bombus carolinus* F. of South America. With these bees, the male corbicular development may have been a response to a stress due to a short active season or a high reproductive rate, or both, and the resulting need for more pollen than that acquired otherwise. Most species of *Boopobombus* have males with moderate corbiculae, the hind fringe of the tibia being nearly always considerably longer than the front one, this suggesting a steering and balancing function.

Sarothrum Fringe

This fringe of long hairs on the hind margin of the sarothrum of the male bumblebees is well developed in the following groups: *Anodontobombus* and *Boopobombus.*

It seems hard to make a rational guess as to the value of these fringes in the former group unless it is merely a part of the general notable hairiness of these bees of the far North, this probably having significance as thermal protection. With the species of *Boopobombus,* however, it is believed that these fringes may be very important in steering and balancing the bees in quick flight guided largely by sight instead of by smell. The very large, flat sarothrum of the honey bee drone, though without a hairy fringe, obviously has this same function.

Field Notes

Early one evening in mid-August, 1929, the writer observed an astonishing swarming of very many males of *B. arcticus* (*hyperboreus*) around a barberry hedge near Charlottetown, Prince Edward Island. In the middle of the day, *B. rufocinctus* was so abundant that it created a nuisance for people in automobiles on the island by coming into open windows.

Interesting material on bumblebee pollination that perhaps

should have been held for the present publishing has been presented elsewhere.[6]

New Subgenera of Bombus

Crotchiibombus, new subgenus

The hind margin of the outer spatha of nearly all the known species of *Boopobombus* is considerably notched or bent forward in the middle. *Bombus crotchii* Cress. is an outstanding exception to this, the outline of the hind margin of the spatha being evenly rounded. This and the almost mossy outer surface of the spatha, because of the numerous spines or hairs it bears, seem reason enough for creating the new subgenus, *Crotchiibombus* for it.

Bombus crotchii (Cress.), of western North America, is the type of this subgenus (present designation).

Several new subgenera probably should be established for South and Central American and Mexican bumblebee species, but these are properly awaiting further study for this.

Statement:

The generic name *Bombus* is used everywhere in this paper instead of *Bremus,* this being considered proper following the decision of the International Commission of Zoological Nomenclature regarding the so-called " Erlangen List ".

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[6] Mass. Agr'l. Expt. Station Bul. 445, 1950, pp. 75 and 76.

THE BIOLOGY OF THE COCKROACH EGG PARASITE, TETRASTICHUS HAGENOWII

(HYMENOPTERA: EULOPHIDAE)[1]

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(Plates I-III, Text-figs.)

Tetrastichus hagenowii (Ratz.) is a small chalcid which is known to parasitize the eggs of several species of cockroaches. It is probably world wide in distribution having been found in eastern and southern United States, the West Indies, South and Central America, Europe, Hawaiian Islands, and the Orient (Burks, 1943).

Relatively little is known of the biology of *T. hagenowii*, and the specific use of this and other hymenopterous egg parasites in cockroach control has not been attempted to any great extent. Cros (1942) liberated a species of *Eulophus* in his home in Algeria for the purpose of controlling the oriental cockroach, but the effectiveness of the parasite in diminishing the cockroach population, as far as we can determine, has not been reported. According to Zimmerman (1948) *Supella supellectilium* (Serv.) was practically wiped out in certain places in Hawaii after the accidental importation of the egg parasite *Comperia merceti* (Compere). Zimmerman distributed the parasite to various parts of Honolulu and successfully controlled the brown-banded roach in a store building; in some surveys he found parasites in nearly 100 percent of all oöthecae located. *T. hagenowii* is an important parasite of eggs of *Periplaneta americana* (L.) and *P. australasiae* (F.) in houses in Formosa (Maki, 1937).

This paper presents some biological data pertaining to *T. hagenowii* and the results of some practical control tests with this parasite.

[1] The writers thank Mr. George Riser, of our laboratory, for his technical assistance, and Dr. Lafe R. Edmunds, U. S. Public Health Service, Mitchell, Nebraska, for the original supply of wasps and for the opportunity of reading his unpublished manuscripts on cockroach egg parasites.

Hosts and Host Specificity

T. hagenowii has been listed as a parasite of at least 6 species of cockroaches representing 5 different genera. We have exposed the eggs of 9 species of cocroaches to these wasps with the following results:

Blattella germanica (L.).—The German cockroach has been listed as a host for this wasp (Burks, 1943; Peck, 1951). However, we have been unable to secure parasitization of the eggs of the German cockroach; nor have we found any original records in the literature in which this wasp has been reared from the eggs of the German cockroach. Normally this cockroach carries its oötheca until or shortly before the eggs hatch (Ross, 1929). Three experiments were run in an attempt to secure parasitized eggs of this species. Seventy-five German cockroaches bearing egg cases were exposed to a large number of wasps (about 65 wasps of both sexes per 10 cockroaches). None of the eggs was parasitized. Twenty-one oöthecae were removed from females and exposed to many wasps. These oöthecae were held until either the cockroach eggs hatched or the egg cases collapsed. The empty egg cases from which the cockroaches had hatched were examined for parasites, and the collapsed egg cases were dissected 2 or more weeks after exposure to the wasps. None of the eggs was parasitized. In a final experiment, 35 oöthecae, manually removed from females, were exposed to several hundred wasps for 4 days at about 90% relative humidity; at this humidity the cockroach eggs lost little water. At the end of 4 days the oöthecae were dissected; no parasite eggs or larvae were found. It is highly questionable that *B. germanica* is a host of *T. hagenowii* in nature.

Blattella vaga Hebard.—*T. hagenowii* did not parasitize the eggs of 2 females of *B. vaga*, a species which also carries its egg case until hatching, and closely resembles the German cockroach. The egg cases were exposed, to 16 female wasps, while still attached to the cockroaches.

Parcoblatta virginica (Brunner).—Seven egg cases of this woodroach were exposed to about 50 female wasps; none of the eggs was parasitized. Edmunds (1953), however, reared *T. hagenowii* from the eggs of *Parcoblatta* sp. collected in the field.

Supella supellectilium.—*T. hagenowii* will oviposit into the eggs of the brown-banded roach but these eggs are not suitable for parasite development. One hundred egg cases of the brown-banded roach were exposed to a large number of wasps. Of these, 61 oöthecae contained some eggs that were parasitized. Usually only a few eggs in any one egg case were parasitized, and these cockroach eggs always failed to develop. Either the wasp eggs failed to hatch, or if they hatched, the larvae died at an early stage of development. Even though the wasps failed to develop to any great extent, the hatching of the unparasitized cockroach eggs was impaired; hatching of some cockroach nymphs occurred in only 6 of the 61 oöthecae that contained some parasitized eggs. Despite this 90% destruction of egg cases, *Tetrastichus* would not be an effective parasite of the brown-banded roach because of the failure of the wasp to complete its development in the eggs of this species.

Eurycotis floridana (Walker).—In the laboratory, *T. hagenowii* will readily oviposit into the eggs of *E. floridana* and develop to maturity. The eggs of this cockroach are rather large and the oötheca contains an average of 23 eggs (Roth and Willis, 1954), so that there is more food per oötheca for the development of more parasites than is provided by the eggs in the oötheca of the American cockroach. For example, each of three *Eurycotis* egg cases, averaging 22.7 eggs, were exposed to 20 female wasps. The mean number of parasite offspring was 648 wasps per egg case; the largest number from one egg case was 685 (664 ♂♂, 10 ♀♀, 11 immatures). On the other hand, each of 4 American oöthecae, averaging 16 eggs and exposed to 20 female wasps, yielded an average of 204 wasps per egg case; the largest number from one egg case was 261 wasps (223 ♂♂, 30 ♀♀, 8 pupae).

Periplaneta americana.—The eggs of this cockroach are commonly parasitized by *T. hagenowii* (Sein, 1923; Bodenheimer (in Klein, 1933); Maki, 1937; Schmidt, 1937; Rau, 1940; and Wolcott, 1951). We have used the eggs of this species to maintain a culture of the wasps in our laboratory, as has Edmunds (1954).

Periplaneta australasiae.—According to Plank (1947) in Puerto Rico the eggs of this cockroach were "parasite free" from *T. hagenowii.* However, Maki (1937) claims that the wasp is an important factor in reducing the numbers of Australian cockroaches

in Formosa. We obtained successful parasitization of a single oötheca [2] of *P. australasiae* exposed to the wasps.

Periplaneta fuliginosa (Serv.).—The wasps successfully parasitized 2 oöthecae of this species of cockroach.

Blatta orientalis L.—Burks (1943) and Peck (1951) list this species as a host for *T. hagenowii.* The wasp also parasitized the eggs of this species in our laboratory; experiments are described below.

The following have also been listed as hosts of *T. hagenowii*:

Neostylopyga rhombifolia (Stoll).—Pemberton (1941) reared *T. hagenowii* from an egg case of this cockroach collected in Manoa Valley, Hawaii.

Evania appendigaster.—For some time *T. hagenowii* was stated to be principally a hyperparasite on the evaniid wasp *E. appendigaster* (Ashmead, 1901; Marlatt, 1902; Perkins, 1913; Lever, 1946). Masi (1917), because of the fact that *T. hagenowii* is widespread and inhabits cockroach oöthecae, believed that this chalcid would parasitize *E. appendigaster* and other genera and species of cockroach egg parasites. It would appear that if *T. hagenowii* were hyperparasitic on *Evania* this relationship would be accidental, the eulophid happening to oviposit into an oötheca already containing the evaniid parasite.

It is apparent that *T. hagenowii* is not as specific in its choice of a host as are certain other cockroach egg parasites. In contrast, *Anastatus blattidarum* Ferr. is apparently specific for *Supella supellectilium* (Flock, 1941), and *Anastatus floridanus* Roth and Willis is specific for *Eurycotis floridana* (Walker), although in the laboratory a small number of the latter wasps oviposited into the eggs of the American and oriental cockroaches (Roth and Willis, 1954).

Experiments were performed in which *T. hagenowii* was given a choice between American and oriental egg cases. The results are shown in Table 1. The wasps showed a preference for the eggs of the American cockroach even though they are capable of developing on oriental eggs. There was little difference between the oviposition preference shown by wasps which had been reared

[2] By parasitized oötheca we imply parasitization of the eggs within the oötheca.

exclusively on American eggs and those reared first on American eggs for several generations and then for 3 generations on oriental eggs.

It is quite possible that in nature there are biological strains of wasps which show a preference for the eggs of one species of cockroach when eggs of other host species are also available. However, if a preferred host is not available, the wasp may oviposit into whatever other cockroach eggs it may find. The existence of biological strains of *T. hagenowii* with different host preferences might explain Plank's (1947) statement that the eggs of *P. australasiae* were not parasitized in Puerto Rico, although Maki (1937) reported this species parasitized in Formosa. A similar phenomenon might be acting with *Anastatus blattidarum.* There are specimens of this wasp from India in the United States National Museum which are said to have been reared from the eggs of *Periplaneta americana* (Burks, 1953); yet Flock (1941) found that *A. blattidarum* which had been reared from *Supella* would not oviposit into the eggs of the American cockroach. It would be interesting to determine the host preference of wasps reared from relatively uncommon hosts parasitized in the field.

Oviposition Behavior

The female wasp crawls over a cockroach oötheca and bends her abdomen ventrally so that the tips of her valvae touch the wall of the egg case (Plate I, A). She walks over the oötheca, repeatedly "testing" the surface; upon finding an acceptable location, the wasp unsheathes her ovipositor and begins to bore through the wall of the egg case (Plate I, B), after which she inserts the sting up to its base (Plate I, C). She can deposit her eggs into the eggs of the cockroach in from 2 to 5 minutes, and the wasp eggs hatch within 24 hours after oviposition (Edmunds, 1954). Frequently after oviposition the female feeds on the material which oozes from the puncture made by her ovipositor (Plate I, D). The larvae (Plate II, A) consume the eggs in which they originally hatched and some of the remaining cockroach eggs which may not have been parasitized.

During the course of our experiments we found 34 empty egg cases into which the wasps oviposited after they had emerged;

Table 1.—Host Selection by Single Females of *Tetrastichus hagenowii* When Given a Choice Between Oöthecae of *Periplaneta americana* and *Blatta orientalis*

Note: Each female was kept in a Petri dish containing 6 cockroach oöthecae (3 American and 3 oriental) for her entire lifetime.

Host Eggs Parasitized by Wasps	Distribution of Wasps According to Host Selected			
	Wasps Reared on American Cockroach Eggs [1]		Wasps Reared on Oriental Cockroach Eggs [2]	
	Number	%	Number	%
American and oriental ..	8	9	14	20
American only	71	79	49	70
Oriental only	11	12	7	10
Total	90	100	70	100

Host Oöthecae	Oöthecae Parasitized			
	Number	%	Number	%
Total parasitized	119	22	131	31
American	98	82	104	79
Oriental	21	18	27	21

[1] Offspring of wasps reared for at least 10 generations [3] on American cockroach eggs.

[2] Offspring of wasps reared for at least 6 generations [3] on American cockroach eggs and then for 3 consecutive generations on oriental cockroach eggs.

[3] These generations were laboratory reared. The original source of the wasps was Batelle Memorial Institute, Columbus, Ohio (Edmunds, 1954).

usually these eggs were deposited on the moist feces left by the larval wasps.

The frequency of oviposition of *T. hagenowii* was determined by exposing single American cockroach egg cases to 43 individual mated female wasps for successive periods of approximately 24 hours each. New eggs were placed with the wasps each day from emergence until they died. No food other than egg material oozing from the oviposition punctures was available to the insects. The results of this experiment are shown in text-figure 1 and table 2, experiment A. Individual wasps laid eggs in 2-9 cockroach egg cases, the mean being 4.8. The wasps did not oviposit

into all the egg cases made available to them but tended to use those offered during the first few days of the experiment. Oviposition was completed by all 43 wasps in from 2-10 days with a mean of 5.9 days. From the data in text-figure 1, it is apparent that over half of the wasps' eggs were deposited during the first 2 days after emergence, with the percentage dropping to 0 by the eleventh day. All of the ovipositing females died by the twelfth day. The mean number of offspring per female wasp was 103.3 (minimum 50, maximum 139).

Table 2.—Number of Oöthecae Parasitized by Single Females of *Tetrastichus hagenowii*

Experiment	Number and Frequency of Oöthecae Parasitized									Total No. Oöthecae Exposed	Total No. Oöthecae Parasitized		Number of Females	Mean No. Oöthecae Parasitized by One Female
	1	2	3	4	5	6	7	8	9		Number	%		
A[1]	0	6	5	4	13	10	3	1	1	353	206	58	43	4.8
B[2]	11	17	5	4	1	0	0	0	0	190	81	42.6	38	2.1
C[3]	18	7	0	0	0	0	0	0	0	125	32	25.6	25	1.3

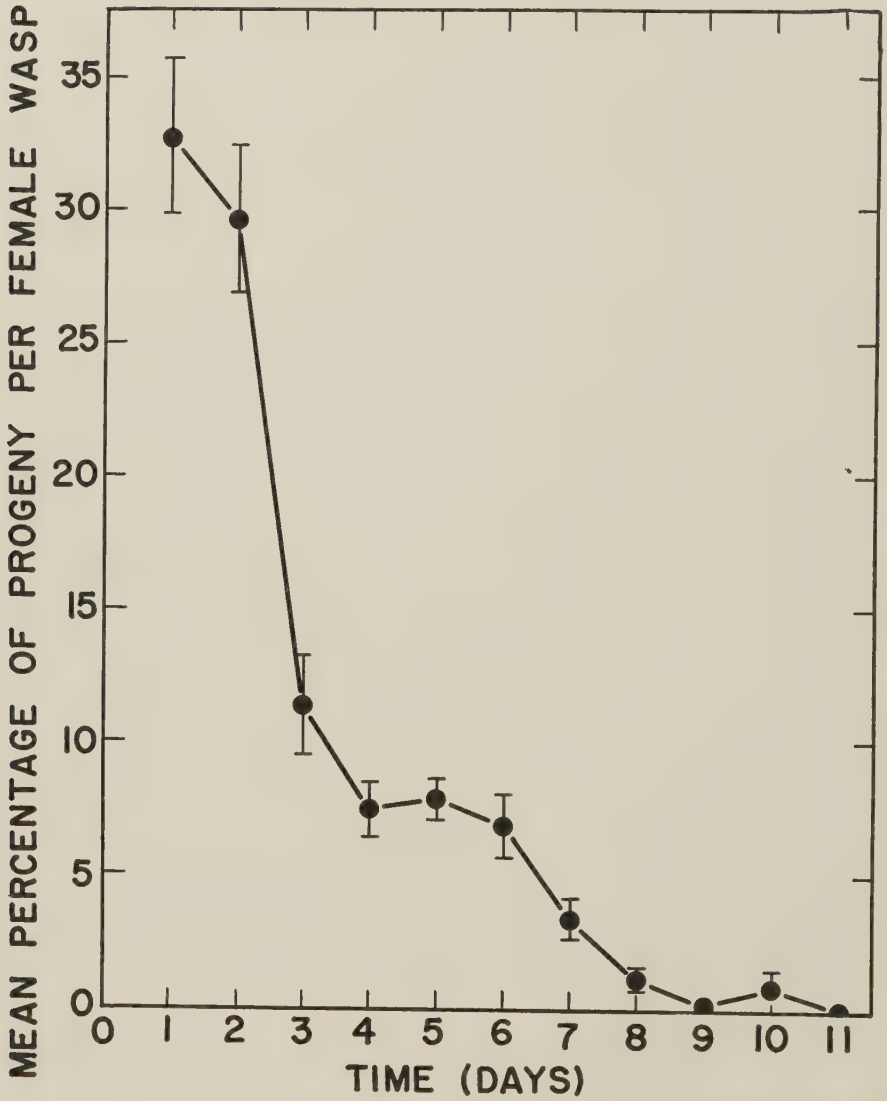
[1] American cockroach oöthecae changed every 24 hours.

[2] Five American cockroach oöthecae left with each female wasp for her entire lifespan.

[3] Five oriental cockroach oöthecae left with each female wasp for her entire lifespan.

In the preceding experiment individual female wasps parasitized the eggs in an average of 4.8 oöthecae when the egg cases were replaced every day. The results, however, are different if females are isolated (in vials or Petri dishes) for their entire lives with several oöthecae.

Thirty-eight wasps were each given 5 American cockroach egg cases at one time (Table 2, experiment B). The average number of parasitized oöthecae was 2.1, yet the average number of offspring per female in this experiment was 94.1, which is very similar to that obtained when the females were given a fresh oötheca every day. In a third experiment in which 25 wasps each were isolated



Text-figure 1.—Frequency of oviposition throughout the lifetime of *Tetrastichus hagenowii* as indicated by the percentage of offspring per day that developed in oöthecae of the American cockroach. The oöthecae were exposed at daily intervals to individual female wasps. The numbers of female wasps for each of the 11 days were 43, 43, 43, 43, 43, 41, 39, 28, 20, 8, and 2 (left to right). The vertical capped lines indicate one standard error.

with 5 oriental cockroach egg cases for the entire lives of the females, an average of only 1.3 oöthecae were parasitized by any one female (Table 2, experiment C). The mean number of offspring per female wasp was 65.8 (minimum 5, maximum 164). In the experiment summarized in table 1 where each female had access to 6 cockroach oöthecae (3 American and 3 oriental) the average number of oöthecae parasitized was 1.3 and 1.9 respectively for the 2 groups of wasps used. It is possible that a female wasp tends to remain with the first one or two oöthecae she finds and oviposits into them over a period of days, rather than selecting a different oötheca each time she deposits some of her eggs.

The size of the adult wasps varies considerably depending on the amount of food available (see below). The size of the adult female may determine, to some extent, the number of eggs deposited and whether or not the female will parasitize the eggs of the cockroach. This effect is shown in table 3 which gives the results of exposing oöthecae to groups of wasps of 3 different sizes. It is obvious that the largest females produce the greatest number of offspring, and that the number of oöthecae parasitized also increases with an increase in the size of the female wasp.

Table 3.—Effect of Size of Ovipositing *Tetrastichus hagenowii* on Number of Oöthecae Parasitized and Size of Brood Produced

Note: Each wasp was given one oötheca of the American cockroach for her entire lifetime.

Length of Wasp Abdomen in Millimeters	Number of Wasps and Oöthecae Exposed	Oöthecae Parasitized		Mean Number of Cockroach Eggs per Parasitized Oötheca	Mean Number ± S.E.[1] of Wasp Offspring per Oötheca
		Number	%		
0.7–0.8	25	8	32	14.7	26 ± 4.0
0.9–1.0	25	19	76	14.4	42 ± 5.3
1.2–1.3	25	24	96	14.8	80 ± 1.5

[1] Standard error.

T. hagenowii will oviposit readily into cockroach oöthecae containing fairly well-developed eggs. Twenty-two American cockroach oöthecae 28-29 days old were exposed to many wasps; all of the oöthecae were successfully parasitized. Twenty-five oöthecae

29 days old were each exposed to single female wasps; 23 of these egg cases were successfully parasitized. Twelve oöthecae 35-36 days old (about 2 or 3 days before hatching) were each exposed to single female wasps; none of these eggs was parasitized. It is possible that the wasps will not oviposit into eggs which are to hatch in a couple of days.

Recently deposited oöthecae will also be parasitized. Two experiments were performed in which single female wasps were offered a choice of two American cockroach oöthecae of different ages; the oöthecae were left with the wasps until the parasites died. The results were as follows:

Experiment 1. Choice between oöthecae 0-1-day old and 14 days old.

None of the oöthecae parasitized	0
Both oöthecae parasitized	11
Only 0–1-day old parasitized	3
Only 14-day old parasitized	11
Total wasps used	25

The wasps will oviposit into recently-dropped oöthecae as well as medium-aged egg cases. Those wasps which selected only one of the two oöthecae offered showed some preference for the older oöthecae.

Experiment 2. Choice between oöthecae 5-6 days old and 12-13 days old.

None of the oöthecae parasitized	5
Both oöthecae parasitized	11
Only 5–6-day old parasitized	19
Only 12–13-day old parasitized	25
Total wasps used	60

The wasps showed no significant preference for oöthecae of either of these age groups.

Development

According to Edmunds (1954) *T. hagenowii* requires 31-60 days to complete its development at 70°-80° F. Edmunds also found that larval feeding (Plate II, A) was completed in 18-25 days. Developmental time is somewhat dependent on the size of the brood in the oötheca; the larger the number of wasps the

shorter the time required to complete development. This relationship, which is shown in text-figure 2, also holds for the cockroach egg parasite *Anastatus floridanus* (Roth and Willis, 1954). Just prior to pupation the larvae void long masses of fecal material in which the caudal ends of the pupae become embedded (Edmunds, 1954). Partial dissections of the oötheca in which the side wall was removed disclosed pupae with their heads apparently all pointing in the same direction (Plate II, C); these parasites had developed while the oötheca was lying on its side. Hence it seemed possible that gravitation might have had some effect on the orientation of the wasp larvae. We therefore placed American oöthecae, containing parasitized eggs, in four different positions in paraffin: (1) with the keel uppermost; (2) with the keel down; (3) with the keel to the side, resting on one of the lateral faces; and (4) with the keel perpendicular, resting on one end.

The oöthecae were oriented, as indicated, about 10 days after exposure to wasps; they were dissected about 3 weeks later by which time the wasp larvae had pupated. Dissections were made at right angles to the long axes of the oöthecae, which enabled us to see the orientation of the wasps most clearly (Plate II, D-G). The pupae were seen to radiate out from a central mass of feces (Plate II, F-G). The posterior ends of the larvae pointed toward the center of the oötheca where the feces were excreted prior to pupation (Plate II, E). Apparently because of the spatial configuration of the interior of the oötheca, the heads of only a few pupae are directed toward the keel. These conclusions are based on oöthecae in which all of the cockroach eggs had been eaten and which were fully packed with wasps. The arrangement described above is not so evident in oöthecae containing few wasps.

Upon completing their development the wasps chew a hole through the wall of the oötheca (Plate III, A and B) and leave the egg case. Usually 1 emergence hole is made in an oötheca but sometimes 2 or 3 holes may be made by the wasps (Table 4).

Oöthecae parasitized by *T. hagenowii* can not be detected from unparasitized oöthecae by gross outward appearance. We were unable to determine parasitization by holding parasitized oöthecae before a bright light, as Edmunds (1952) did with oöthecae parasitized by evaniids. However, Watanabe (1953) of our laboratory

has found that, except during the first and fourth weeks of development, the rates of oxygen uptake are considerably higher for cockroach egg cases containing *T. hagenowii* than for unparasitized egg cases. She suggested that, with egg cases of unknown history, the measured rate of oxygen uptake can be used as a criterion of parasitization during the second and third weeks of wasp development.

Table 4.—Number of Emergence Holes Made by *Tetrastichus hagenowii* in the Oöthecae of 3 Species of Cockroaches

Oöthecae of	Number and Frequency of Emergence Holes			Total No. Oöthecae	Mean Number of Emergence Holes
	1	2	3		
P. americana	303	44	4	351	1.2
B. orientalis	50	14	5	69	1.4
E. floridana	9	8	1	18	1.6

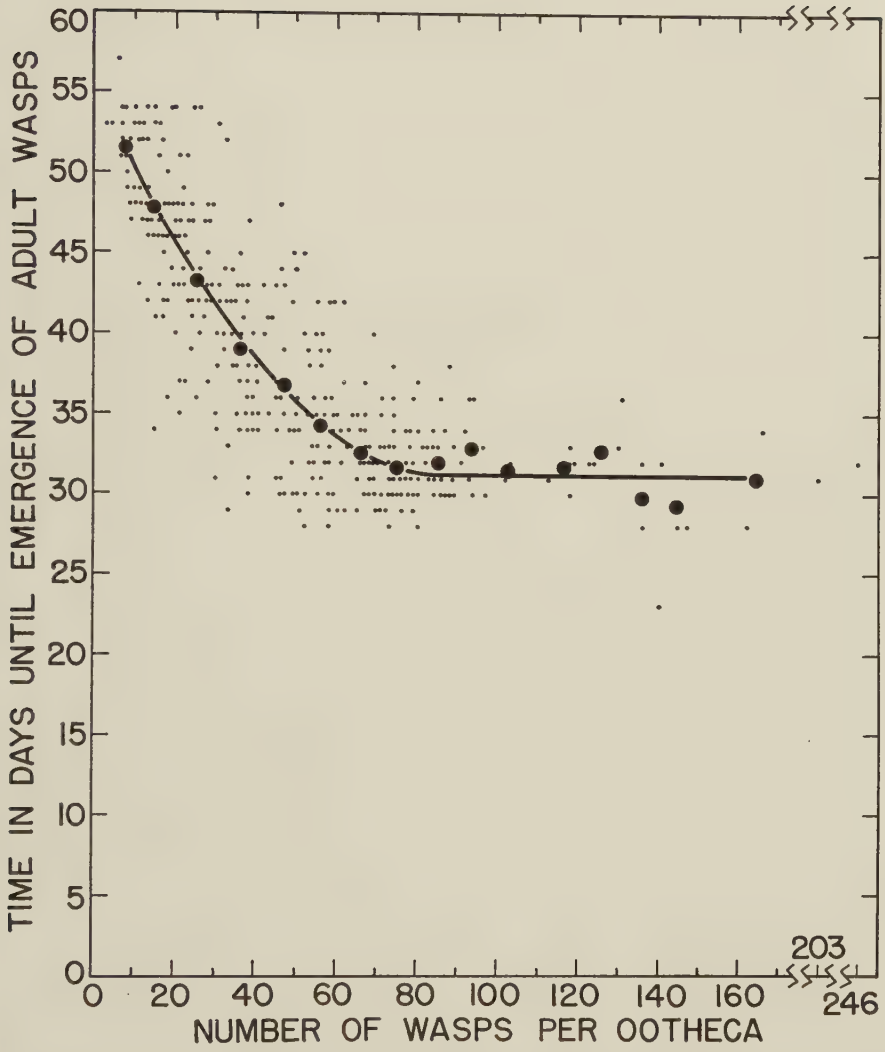
Size of Adult Wasps

The size of the adult wasps may vary considerably and is determined, at least in part, by the number of parasites developing within the oötheca. The fewer the wasps developing within an egg case, the more food is available to the larvae, and the resulting adults are larger than they would otherwise be. The relationship between the number of parasites developing in three oöthecae and the size of the emerging adult wasps is shown in table 5.

Table 5.—Relationship Between the Number of Parasites Developing Within an Oötheca of *P. americana* and the Size of the Emerging Adult Female Wasps

Number of Wasps Emerged from Oötheca	Mean Length ± S.E. (mm.) of		Number of Wasps Measured
	Antenna [1]	Hind Tibia	
28	0.76 ± 0.003	0.68 ± 0.003	20
102	0.66 ± 0.003	0.57 ± 0.001	20
203	0.53 ± 0.015	0.44 ± 0.017	20

[1] Pedicel and funicular segments.



Text-figure 2.—Time required for *Tetrastichus hagenowii* to complete development and emerge from oöthecae of the American cockroach, as a function of the number of wasps per oötheca. Each small dot represents observed data from one or more parasitized oöthecae. The larger circles are means computed from these data after grouping in increments of 10 wasps; a total of 457 parasitized oöthecae were used.

Sex Ratio and Parthenogenesis

The sex ratios of the offspring from individual mated females are given in table 6. The average ratios varied from about 2 females to 1 male to as high as 8 females to 1 male. From 4 oötheca more males than females emerged, and in 1 oötheca, only females developed. In general the offspring from a mated female were preponderantly female.

Table 6.—Sex Ratios of Offspring of Single, Mated Females of *Tetrastichus hagenowii*

Note: Values based on samples in which all wasps developed and hatched; no larvae or pupae remained in the oöthecae.

Number of Wasps per Oötheca		Number of Parasitized Oöthecae	Average Sex Ratio ♀♀ : ♂
Range	Mean		
7–10	8.2	6	4.4 : 1
11–20	15.0	32	4.8 : 1
21–30	24.2	22	5.8 : 1
31–40	35.9	17	4.6 : 1
42–50	45.5	12	6.9 : 1
51–60	57.6	8	7.5 : 1
61–67	64.6	11	6.0 : 1
71–80	74.9	18	3.7 : 1
81–84	82.2	4	2.2 : 1

The sex ratio of any generation from mated female Hymenoptera may be changed by differential mortality of eggs and larvae (Flanders, 1945). Though the ratios shown in table 6 are based on broods in which no immature individuals remained in the oötheca, it is quite possible that there was some mortality because of cannibalism among the larvae. Indirect evidence that cannibalism does occur was obtained by exposing single oriental oöthecae to different groups of 5 female wasps; two groups of egg cases were dissected at 9 and 14 days after exposure to the females, and one group was allowed to mature and hatch. The results are shown in table 7. More wasps were found at the initial count at 9 days than later; there was a significant drop in the number of wasps on the 14th day, after which there was essentially no change. The data suggest that cannibalism may occur if the population density in an oötheca is too high for the available food. Similar results were found with the cockroach egg parasite *Anastatus floridanus* (Roth and Willis, 1954).

Table 7.—Reduction in Density with Time, of Offspring of *Tetrastichus hagenowii* Developing in Oriental Cockroach Oöthecae

Days After Exposure of Oöthecae to ♀ Wasps	Mean Number ± S.E. of Wasps per Oötheca	Developmental Stage of Wasps	Number of Oöthecae
9	228 ± 21	larvae	5
14	126 ± 19	larvae	5
33–47	130 ± 8	adults + unhatched immatures	5

Edmunds (1954) found one egg case from which 64 male but no female wasps emerged; he concluded that this might indicate parthenogenetic reproduction. *T. hagenowii* will develop parthenogenetically producing only males. This was determined by removing unmated, adult female wasps from two American cockroach oöthecae. Just prior to emergence of the adult wasps these egg cases were kept cooled on ice to immobilize the wasps, and thus prevent mating when the insects were removed from the oöthecae. Ten American and 5 oriental cockroach egg cases were exposed to 55 unfertilized female wasps. Of these, 5 American and 4 oriental egg cases were parasitized. A total of 1318 wasps emerged from these 9 oöthecae; all were males (arrhenotoky).

Effect of Parasite Density on Host

When sufficient numbers of wasps develop in an oötheca all of the cockroach eggs are eaten (Plates II and III, C). However, if too few parasite larvae are feeding, some of the cockroach eggs will not be eaten (Plate II, B); these eggs complete their development and hatch. This was especially true of the last oöthecae to be offered to the wasps, after they had oviposited into several other egg cases. The relation of parasite density to the destruction or hatching of cockroach eggs is shown in table 8. All of the cockroach eggs were eaten when there was an average of 48 wasps per oötheca.

With an average of 18 wasps per oötheca not all of the cockroach eggs were eaten. However, the uneaten eggs in these oöthecae failed to hatch even though some completed their development. Inasmuch as hatching depends on the combined efforts of all of the

Table 8.—Effect of Parasite Density on Hatching of American Cockroach Eggs

No. of Oötheca	Mean No. Wasps per Oötheca	Mean No. Cockroaches Hatching per Oötheca	Mean No. Cockroach Eggs per Oötheca	Mean No. Cockroach Eggs Eaten by Wasp Larvae
Each egg case kept with one female wasp for 24 hr. period				
35	48	0	14.8	14.8
130	18.3	0	15.3	10.0
28	7.9	8.4	15.5	4.8
Each egg case kept with one female wasp for her entire lifetime				
67	69.3	0	15.1[1]	15.1[1]

[1] These values based on 50 egg cases.

cockroach embryos to split the seam of the oötheca, undoubtedly these uneaten embryos fail to hatch because there are too few cockroaches remaining in the oötheca to force the seam apart. With an average of 8 wasps per oötheca only about 5 cockroach eggs were destroyed; apparently a sufficient number of developed embryos remained in these oöthecae to split the seam.

Practical Control Tests

Three experiments were performed in which cockroach oöthecae were distributed in rooms, and wasps were liberated to determine the percentage of egg cases that would be parasitized. Two rooms were used, one a laboratory 16 ft. × 17 ft. × 13 ft., and the other a basement in a private home. In the laboratory the oöthecae were distributed on shelves and in crevices, from near floor level to areas close to the ceiling; in the basement the egg cases were distributed around boxes and other materials lying around. The wasps were liberated on the floor approximately in the center of the rooms. The results are shown in table 9. A fairly high percentage of eggs were parasitized particularly when the ratio of wasps to oöthecae was about 10:1. The wasps found and oviposited into the eggs located in all parts of the rooms—including those located near the ceiling of the laboratory room.

In experiment A the oöthecae were kept until the wasps or cockroaches hatched. Cockroaches hatched from only 1 oötheca con-

taining some parasitized eggs. Wasps hatched out of 34 of the 80 oöthecae that contained parasites; in the 46 parasitized oöthecae from which the wasps failed to emerge, most of the parasites completed their development but failed to chew their way out of the egg cases, but many died as larvae. It is possible that unusually high summer temperatures may be harmful to the wasps and were responsible for the high mortality. This was indicated by high mortality and failure of many of the wasps in the stock colony to oviposit during July and August when the temperature at times was in the high nineties and even went above 100° F.

In experiment B the oöthecae were dissected 9 days after exposure; in experiment C the oöthecae were dissected 12-14 days after exposure.

Table 9.—Results of Liberating *Tetrastichus hagenowii* into Rooms Containing Cockroach Oöthecae

Experiment	Oothecae[1] Distributed		Approximate No. ♀ Wasps Liberated	Oöthecae Parasitized	
	Number	Species		Number	%
A[2]	96	American	1000	80	83%
B[2]	101	American	800	75	74%
	71	Oriental		40	56%
C[3]	89	American	450	25	28%

[1] Does not include oöthecae that contained cockroach eggs which showed no development if the eggs were unparasitized.

[2] Oöthecae and wasps distributed in a laboratory room.

[3] Oöthecae and wasps distributed in basement of private home.

Summary

Tetrastichus hagenowii will parasitize and successfully develop in the eggs of *Periplaneta americana, P. australasiae, P. fuliginosa, Blatta orientalis, Eurycotis floridana, Parcoblatta* sp., and *Neostylopyga rhombifolia.* The wasp will oviposit into the eggs of *Supella supellectilium,* but the parasite's eggs fail to hatch, or if they do, the larvae die at an early stage of development. In experiments reported herein the wasps failed to ovipost into the eggs of *Blattella germanica, Blattella vaga,* and *Parcoblatta virginica.* The parasite may complete oviposition in 2 to 10 days the average being about

6 days. Over half of the wasp's eggs are deposited during the first 2 days after emergence. The female produces about 100 offspring. When given a fresh oötheca every 24 hours, the female parasitizes an average of 4.8 oöthecae. However, when confined with 5 oöthecae for her entire lifetime, only an average of 2 egg cases are parasitized. The size of the female wasps may vary considerably depending on the number of wasps developing in the egg case; the larger the number of wasps the smaller the size of the resulting adults. The largest females produce the greatest number of offspring, and the smaller the female the less likelihood that she will parasitize the cockroach eggs. *T. hagenowii* will oviposit into, and its eggs will develop in, recently-dropped oöthecae as well as in eggs about a month old. Development takes from 23 to 56 days at temperatures about 85° F. or higher. The developmental time of wasps in broods averaging less than 60 individuals is generally longer than the developmental time for broods averaging more than 70 individuals. With an average of 48 wasps per oötheca all of the cockroach eggs are eaten. With an average of 18 wasps per oötheca not all of the cockroach eggs are eaten but the uneaten eggs fail to hatch. With an average of 8 wasps per oötheca an average of about 8 cockroaches hatch from the parasitized egg case. The sex ratio of the offspring from mated females may vary from 2 ♀ : 1 ♂ to about 8 ♀ : 1 ♂ ; there is usually a preponderance of females. Only males are produced from eggs laid by unmated females. When *Tetrastichus* was liberated in a room in which cockroach oöthecae had been distributed, as high as 83% of the egg cases were parasitized when the ratio of female wasps to oöthecae was 10 : 1.

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Explanation of Plates

Plate I.

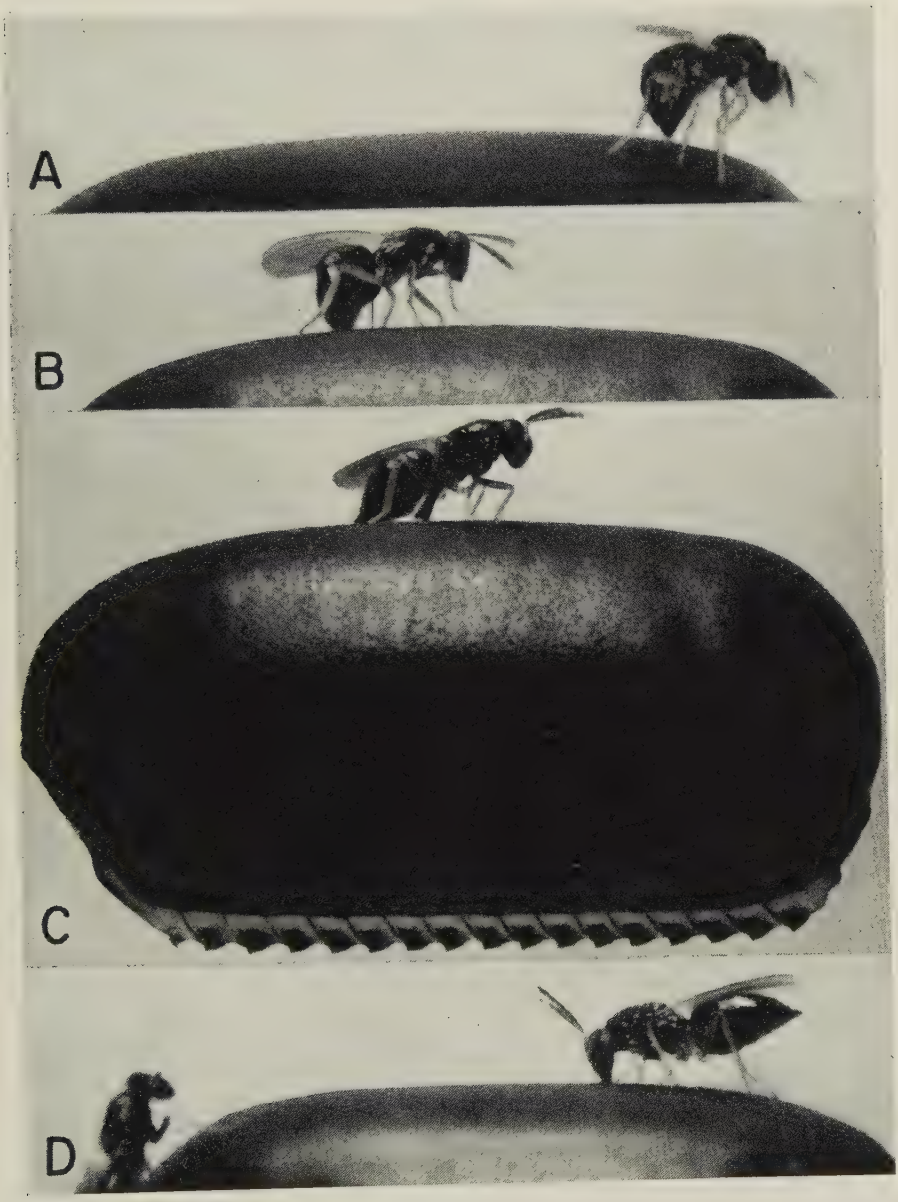
Oviposition behavior of *Tetrastichus hagenowii*. X 12.1. A.—Wasp "probing" the surface of an American cockroach oötheca with the tips of her valvae. B.—Wasp beginning to penetrate the oötheca with her unsheathed ovipositor. C.—Wasp with ovipositor inserted up to its base into the oötheca. D.—Wasp feeding on material which oozed from the oviposition puncture.

Plate II.

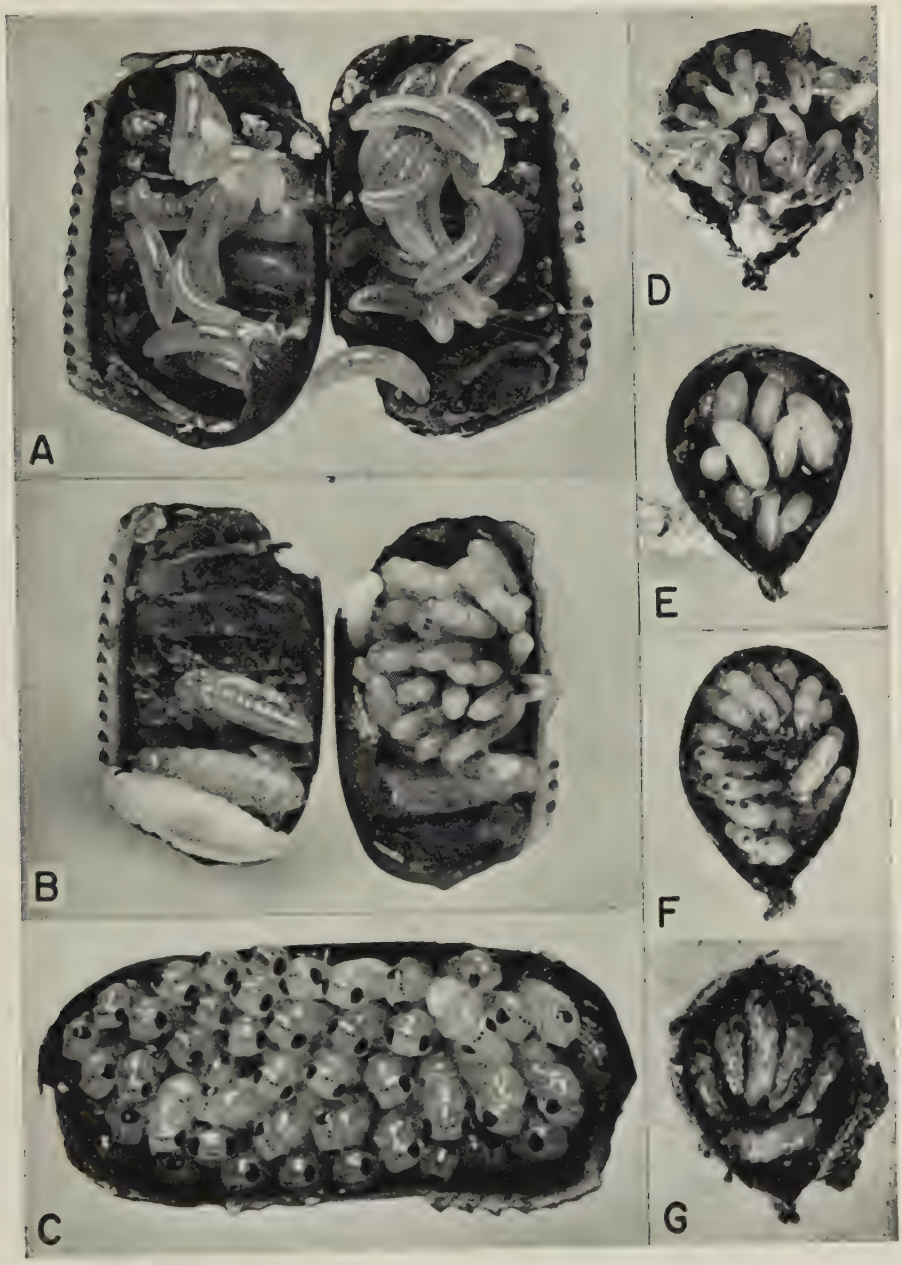
Immature stages of *Tetrastichus hagenowii*. A-C.—American cockroach oöthecae cut open at indicated times after exposure to ovipositing wasp. A.—Well-developed wasp larvae at 9 days; most of the cockroach eggs have been eaten. X 6.1. B.—Wasp larvae and pupae at 38 days with several uneaten fully developed cockroach embryos. X 6.1. C.—Oötheca at 30 days packed with wasp pupae; note the pigmented eyes and ocelli of each pupa and the fact that practically all of the pupae in view are oriented in more or less the same direction. X 9.5. D-G.—Parasitized oöthecae cut in cross section (keel down). X 6.6. D.—Young larvae which have not yet oriented. E.—Mature larvae which have oriented with their heads towards the wall of the oötheca; feces have already been voided. F-G.—Pupae showing typical orientation. In F the mass of feces may be seen in the center at the posterior ends of the pupae.

Plate III.

Oöthecae of the American cockroach in which *Tetrastichus hagenowii* developed. A.—Adult wasp emerging from a hole chewed through the wall of the oötheca. X 9.4. B—Oötheca with a single round emergence hole. X 9.4. C.—Oötheca in B opened to show the complete destruction of cockroach eggs by the wasps which had already emerged. X 8.



ROTH AND WILLIS—COCKROACH EGG PARASITE



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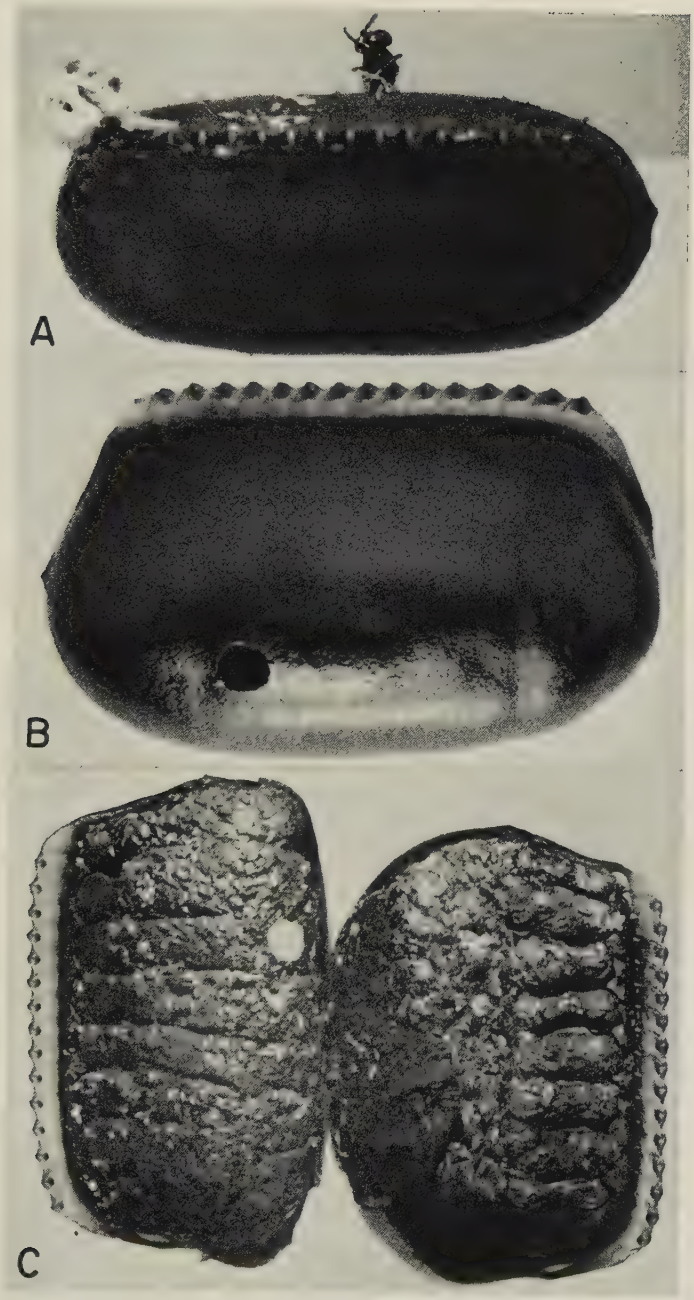

ROTH AND WILLIS—COCKROACH EGG PARASITE

A REVISION OF THE SPECIES INCLUDED IN THE GENUS NOVELSIS

(COLEOPTERA: DERMESTIDAE)

BY R. S. BEAL, JR.

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(Text-figures)

The genus *Novelsis* was erected by T. L. Casey in 1900 for the reception of a group of beetles previously included in *Attagenus*. Though some subsequent authors have not accepted the separation of *Novelsis* from *Attagenus*, it is most probable that the two represent phylogenetically distinct lines. As much is indicated by the uniformity of male and female antennal structure in each group as well as by the larval characters pointed out by Rees (1943). The uniformity of antennal structure is not, however, wholly as Casey conceived. He thought the two genera might be separated by the total number of segments in the antenna of the male. Unfortunately, in each genus are found species with ten-segmented antennae and species with eleven-segmented antennae. Rather, constant generic characters are found in the structure of the antennal club. In species of *Novelsis* the segments of the antennal club of both sexes are loosely joined, not compact as in *Attagenus*. In the male the first two segments of the club are subequal in length to the last, whereas in males of *Attagenus* the ultimate segment greatly exceeds in length the two preceding.

Actually, the species assigned here to *Novelsis* make up several groups which should be raised to generic level. However, it is felt that further generic designations should not be made until there is opportunity to restudy the Attageninae of the world and relate our American species to such genera as *Adelaidea*, *Telopes*, and *Lanorus*. The purpose of this paper is not to develop the generic relationships of the group, but to provide a basis for a better understanding of the species involved. Casey's division of the genus

into two subgenera is not followed here for the same reason, and for the fact that the two subdivisions are not adequate for the species now known.

Details of the biology of this genus are scanty. Adults of *uteana* have been collected on *Tamarix gallica,* on *Prosopis* sp., and on *Melilotus* sp. *N. andersoni* has been taken on *Atriplex lentiformis.* Adults of two species, *picta* and *varicolor,* have been taken at lights. The larvae are most likely general scavengers of dried animal protein, much like various species of *Attagenus. N. horni* and *varicolor* larvae have been found in old mud dauber wasp nests, and a *horni* larva has been taken from a Leptochiline-like wasp nest in a sand bank (Beal, 1951). A good number of *varicolor* larvae were found in a hen's nest at Presidio, Texas, by J. H. Russell.

It is fairly easy to assess the relationships which the various species bear to one another. This can be done by noting the similarities and differences in certain morphological structures which seem to be rather stable throughout the family. The most important of these are the following: proportions in the female antennal club, the character of the pubescence clothing the male antennal club, the presence or absence of rows of spines on the tibiae, and the relative width of the metacoxal lamina. The validity of relating species on the basis of the foregoing characters is confirmed by simlarities in the patterns of elytral maculation and pubescence in the species so related. On the other hand, the number of segments in the antenna does not seem to be a character of any value in determining phylogenetic relationships, either in the Attageninae or in other sections of the Dermestidae. Other characters, particularly those of the larval stages, have yet to be thoroughly studied.

These characters align the species in three distinct groups. The first group consists of *perplexus, varicolor,* and *aequalis. Athlophora* apparently belongs to a group by itself, although it possesses some characters in common with the preceding group and the one which follows. The pubescence of the male antennal club is quite like that of *picta,* while the lateral margins of the pronotum and the surface of the hypomeron are quite similar to those of *perplexus.* The third group is formed by the remaining species, *picta, uteana, horni, andersoni,* and *timia.*

NOVELSIS Casey

Novelsis Casey, 1900, Jour. N. Y. Ent. Soc., 8:144.—Dalla Torre, 1911, Junk Col. Cat., 33:59.—Rees, 1943, U.S.D.A. Misc. Pub. Soc., 115:4, 9.
Novelsis (*Paranovelsis*) Casey, 1900, Jour. N. Y. Ent. Soc., 8:148.
Genattus Sharp, 1902, Biol. Centr.-Amer., Col. 2(1):546.
Attagenus, Sharp, 1902, Biol. Centr.-Amer., Col., 2(1):645.—Hinton, 1945, Beetles assoc. with stored prod., 1:305.

Adult Male.—Antenna with ten or eleven segments; antennal club three-segmented with segments not compactly joined; first and second segments of club subequal in length; combined length of first and second segments subequal to length of third segment. Hypomeron not margined behind; surface slightly convex to strongly concave. Mesosternum sulcate anteriad; sulcus not extending to posterior margin. Tarsi with or without short spines along dorsal margins. First segment of metatarsus less than half as long as second segment.

Adult Female.—Segments of antennal club subequal, or first and second segments subequal with a combined length subequal to length of third segment.

Type of genus.—Attagenus horni Jayne.

Key to Males of Species of Novelsis

1. Integument uniformly dark brown; pubescence unicolorous, black with golden sheen; antenna ten-segmented; metacoxal lamina extended laterad to margin of metepimeron ..... **athlophora**
   Integument brown and pubescence whitish, or integument dark with light maculations or with patterns of light and dark hairs; antenna ten- or eleven-segmented; metacoxal lamina extended laterad no further than middle of hind margin of metepisternum 2
2. Antenna 11-segmented 3
   Antenna 10-segmented 7
3. Hypomeron strongly concave, forming deep antennal fossa 4
   Hypomeron flat or slightly convex 5
4. Elytral integument black or piceous with ill-defined brown or reddish-brown area on basal two-thirds of elytron and occasionally with a reddish subapical spot; a patch of white pubescence usually present on apical margin behind subapical band of light pubescence ..... **aequalis**
   Elytral integument with light tan or light piceous maculae; no patch of white pubescence usually present on apical margin of elytra behind subapical spot of light pubescence ..... **varicolor**
5. A sutural line of light maculation present extending at least to apical fifth of elytra; no submedian or apical bands of light maculation or light pubescence present on elytra 6
   No sutural line of light maculation present on middle of elytra; elytra with a subbasal band, a postmedian band, and an apical area of light pubescence ..... (male of **timia**?)

6. Marginal line of light maculation extending to about posterior third or fourth of elytron ..... **andersoni**
   Marginal line of light maculation, if present at all, not extending behind middle of elytron ..... **horni**
7. Antenna in repose extending almost to lateral hind margin of metasternum **picta**
   Antenna in repose extending no further than hind margin of pronotum ..8
8. Integument of elytra somewhat lighter in color than that of pronotum; elytron marked with sutural line and antemedian, oblique band of light pubescence, and sometimes other thin, longitudinal, lateral lines of light pubescence ..... **uteana**
   Pronotum and elytra black; elytron marked with incomplete basal circle, one or two submedian patches, a subapical patch, and an apical patch of light pubescence ..... **perplexa**

Key to Known Females of Species of Novelsis

1. Antenna 11-segmented 2
   Antenna 10-segmented 5
2. A sutural line of light maculation extending at least to apical fifth of elytra; no transverse bands of light maculation or spots of light pubescence evident behind middle of elytra ..... **horni**
   Elytra with definite spots or bands of light maculation or light pubescence behind middle 3
3. Surface of hypomeron flat or only very slightly concave, not forming a fossa for the reception of the antenna ..... **timia**
   Surface of hypomeron concave for entire length of pronotum, forming a fossa for the reception of the antenna 4
4. Elytral integument almost entirely black or black with ill-defined, dark red area on basal two-thirds of elytron and occasionally with a reddish, subapical spot; a patch of white pubescence usually present on apical margin behind subapical band of light pubescence ..... **aequalis**
   Elytral integument with tan or light piceous maculae; no patch of white pubescence usually present on apical margin of elytra behind subapical spot of light pubescence ..... **varicolor**
5. Elytra with light pubescence over entire surface; integument of elytra medium brown to buff without well-defined maculae ..... **uteana**
   Elytra with light pubescence limited to well-defined bands and lines or spots; integument piceous to black, with or without light maculae 6
6. Light maculation or areas of light pubescence forming an incomplete basal circle, a broken submedian band, a subapical spot or band, and an apical spot ..... **perplexa**
   Light maculation and light pubescence forming a sutural line extending length of elytra, an antemedian oblique band and a marginal line extending from base to apical third of elytron ..... **andersoni**

Description and Discussion of Species

Novelsis perplexa (Jayne)

Attagenus perplexus Jayne, 1882, Proc. Amer. Philo. Soc., 20:356.—Dalla Torre, 1911, Col. Cat., 33:55.
Novelsis perplexa, Casey, 1900, Jour. N. Y. Ent. Soc., 8:149.

Adult Male.—Color of head and pronotum black to piceous; elytra black to dark brown, with or without lighter, reddish-brown maculae corresponding in pattern to areas of light pubescence; undersurfaces black to piceous; legs and antennae piceous to medium brown. Pubescence of dorsal surfaces of black, golden or golden-brown, and white hairs; light colored hairs of each elytron forming a basal circle or "loop," a short or broken submedian band, a short subapical band, and a small apical spot; hairs subrecumbent, moderately coarse; hairs along margins of elytra erect, about one and one half times as long as hairs on disc; pubescence of ventral surfaces moderately coarse, recumbent, whitish and golden-brown. Antenna ten-segmented; total length of first two segments of club about one-sixth longer than length of ultimate segment; segments of club densely clothed with very fine, erect pubescence, the individual hairs about two-thirds as long as width of third segment of antenna. Lateral margin dividing hypomeron and pronotum carinate; surface of hypomeron slightly concave between lateral margin and prosternum. Epipleuron transversely horizontal, or nearly so, for most of length, terminating about middle of first abdominal sternite. Metacoxal lamina extended no further than middle of hind margin of metepisternum. Legs moderately stout; tibiae armed on dorsal margin with short spines; protibiae slightly clavate. Length (of pronotum and elytra) varying from 3.0 mm. to 3.8 mm. Ratio of length to width (at humeri) varying from 1:0.54 to 1:0.58.

Adult Female.—First two segments of antennal club subequal; first or second segments one half to three fifths as long as terminal segment. Length (of pronotum and elytra) varying from 4.0 mm. to 4.8 mm.

Type locality.—Nevada. Lectotype in the Academy of Natural Sciences of Philadelphia.

New records.—British Columbia: Peachland, July 24, 1919 (J. B. Wallis). California: Castle Crag, July 28, 1898 (A. Fenyes collection); Davis Creek, Modoc County, July 11, 1922 (C. L. Fox); Fallen Leaf Lake, July 23, 1915 (Van Dyke collection), July 26, 1937 (E. S. Ross); Hat Creek, Shasta County, July 11-30, 1952 (G. Pronin); Huntington Lake, July 25, 1937 (A. T. McClay); Idyllwild, San Jacinto Mountains, July 6, 1950 (R. Schuster); Sisson, July 26, 1918 (E. P. Van Duzee). Utah: Reno (Liebeck collection). Washington: Leavenworth, July 7-9, 1933 (Wickham); Soda Springs, 1933 (Wickham).

This species apparently is the only member of the genus occurring at higher elevations along the Pacific Coast. One other species, *athlophora,* is found in the Pacific Northwest (in Idaho), but is not likely to be confused with *perplexa.*

Novelsis varicolor (Jayne) (Fig. 3.)

Attagenus varicolor Jayne, 1882, Proc. Amer. Philo. Soc., 20:357.
Novelsis varicolor, Casey, 1900, Jour. N. Y. Ent. Soc., 8:149.—Dalla Torre, 1911, Col. Cat., 33:59.—Beal, 1951, Pan. Pac. Ent., 27:57.

ADULT MALE.—Color of head and pronotum black; elytra black with apices black to piceous, and with variable light tan to light piceous maculae (cf. discussion); undersurfaces black; antennae and legs piceous to brown. Pubescence of dorsal surfaces of black or piceous and white hairs with a few golden-brown hairs; hairs subrecumbent to suberect, moderately coarse; hairs along margins of elytra one and one half to two times as long as hairs on disc; light colored hairs of elytron forming more or less complete basal circle, submedian band, and subapical band; pubescence of ventral surfaces moderately coarse, recumbent, white. Antenna 11-segmented; configuration of antennal club as illustrated; segments of club densely clothed with very fine, erect pubescence, the individual hairs about two-thirds as long as width of third segment of antenna. Lateral margin dividing hypomeron and pronotum forming knife-like carina; surface of hypomeron strongly concave between lateral margin and prosternum. Epipleuron transversely oblique for most of length, forming only slight angle with vertical side of elytron, extending beyond hind margin of first abdominal sternite. Metacoxal lamina barely attaining inner margin of metepisternum. Legs moderately stout; tibiae armed on dorsal margin with short spines; protibiae slightly clavate. Length (of pronotum and elytra) varying from 2.6 mm. to 3.1 mm. Ratio of length to width (at humeri) varying from 1:0.47 to 1:0.57.

ADULT FEMALE.—First two segments of antennal club subequal; first or second segment one half to three fifths as long as terminal segment. Length (of pronotum and elytra) varying from 2.9 mm. to 3.8 mm.

Type locality.—Originally published as "Pacific States," but the lectotype bears the label "Cal." Lectotype in the Academy of Natural Sciences of Philadelphia.

Records at periphery of known distribution.—CALIFORNIA: El Centro. ARIZONA: Boulder Dam, Globe, Carr Canyon, Huachuca Mountains. TEXAS: Presidio. Adults collected in March through June.

This species is easily separated from all others in the genus except *aequalis,* which it closely resembles in all but a few characters. It is most easily distinguished from *aequalis* by the light tan or light piceous area on each elytron. This area is usually more or

less sharply defined, whether it is reduced and irregular or whether it occupies all of the elytron except for a narrow, black border. *Aequalis*, in contrast, bears an ill-defined, brown or reddish-brown macula on each elytron. The two may be separated as well by the structural characteristics of the epipleuron, although these differences are somewhat difficult to describe for the worker who does not have specimens of both species for comparison. In *varicolor* the epipleuron is more oblique than it is in *aequalis*, forming a more obtuse angle with the adjacent, vertical side of the elytron. In addition, the margins of the epipleuron in *varicolor* are usually continued distinctly beyond the hind margin of the first abdominal sternite, whereas in *aequalis* the epipleuron usually ends distinctly before the margin of the first abdominal sternite.

Possibly these two forms do not deserve separate specific status, especially in view of the geographic variability observed in *varicolor*. However, since the forms are separated by a fair geographical distance (at least on the basis of present collections) and since no intermediate connecting forms are known, it seems safest to treat them as separate species.

On the other hand, it is possible that *varicolor* may represent a complex of more than one species. *Varicolor* certainly exhibits a wider degree of variation than is observed in any other species of *Novelsis*. This variation is evident in the proportions of length to width in various specimens and in the patterns of elytral maculation. The variations in proportion of length to width do not seem to be correlated with the geographic distribution of the forms, while the variations of pattern are, at least to a certain extent. The variations in pattern which have been observed are the following. In a series of specimens from Presidio, Texas, the area of light maculation is a light piceous and occupies most of the elytron. This form bears the greatest resemblance to *aequalis*. A short series of similar appearing specimens has been taken at Miami, Arizona. Other specimens have been taken from southern and western Arizona and from El Centro, California. All of these have maculae of a light tan color, although the maculae may be considerably reduced and interrupted or may occupy most of each elytron. Many of the specimens studied are from old collections, and though labeled " Tucson " or " Phoenix," may have been taken

either in the immediate vicinity of these cities or in the adjacent mountains. It is possible that the various forms may be found to be closely correlated with various ecological stituations. Precise information on this point will have to await future collections.

Novelsis aequalis (Sharp), new combination

Genattus aequalis Sharp, 1902, Biol. Centr.-Amer., Col., 2(1) :646.
Attagenus aequalis, Hinton, 1945, Beetles assoc. with stored prod., 1 :305.

Adult Male.—Color of head black; pronotum and elytra black to piceous with suffused, brown or reddish brown maculae on elytra; undersurfaces black to piceous; antennae and legs piceous to brown. Pubescence of dorsal surfaces of black, golden-brown, and white hairs; hairs subrecumbent to suberect, moderately coarse; hairs along margins of elytra one and one half to two times as long as hairs on disc; light colored hairs of elytron forming basal circle, submedian band, and subapical band, usually with addition of a few light hairs or spot of light hairs at apex; pubescence of ventral surfaces moderately coarse, recumbent, white. Antenna eleven-segmented; configuration of antennal club as illustrated for *varicolor*; segments of club densely clothed with very fine, erect pubescence, the individual hairs about two thirds as long as width of third segment of antenna. Lateral margin dividing hypomeron and pronotum forming knife-like carina; surface of hypomeron strongly concave between lateral margin and prosternum. Epipleuron somewhat transversely oblique for most of length, forming obtuse angle with adjacent, vertical side of elytron, rarely extending posteriad as far as hind margin of first abdominal sternite. Metacoxal lamina barely attaining inner margin of metepisternum. Legs moderately stout; tibiae armed on dorsal margin with short spines; protibiae slightly clavate. Length (of pronotum and elytra) varying from 2.6 mm. to 3.2 mm. Ratio of length to width (across humeri) varying from 1 :0.55 to 1 :0.59.

Adult Female.—First two segments of antennal club subequal; first or second segment one half to three fifths as long as terminal segment. Length (of pronotum and elytra) plus or minus 3.4 mm.

Type locality.—Mexico.

New records.—Texas: Beeville, May 15, 1912 (H. P. Wood) : Brownsville, July 6, 1895 (Hubbard and Schwarz) ; Cypress Mill (Chittenden) ; Fedor (Lee County) (H. Klages collection) ; Kerrville, June 5, 1905, June 17, 1908 (F. C. Pratt) ; New Braunfels (Liebeck collection) ; San Antonio, June 22, 1895 (H. Soltau) ; Uvalde County, May 11, 1946 (D. J. and J. N. Knull). Mexico: Cordoba, Veracruz (A. Fenyes) ; April 15, 1908 (Fred K. Knab) ; Matomoros, Puebla, May 14, 1942 (Bibby and Moreno).

Novelsis athlophora new species (Fig. 3.)

ADULT MALE.—Color of head and pronotum dark brown; elytra and undersurfaces somewhat lighter brown. Pubescence of dorsal surfaces fine, uniformly dark brown, suberect; hairs along lateral margins of elytra one and one third to one and two thirds times as long as hairs on disc; pubescence of ventral surfaces shorter, fine, brown, subrecumbent. Antenna ten-segmented; configuration as illustrated; antennal club densely clothed with short fine pilosity. Lateral margin dividing hypomeron and pronotum carinate; surface of hypomeron only very slightly concave between lateral margin and prosternum. Epipleuron transversely horizontal for entire length. Metacoxal lamina extended laterad to inner, posterior angle of metepimeron. Tibiae of legs slender, not armed with stouter spines except at apices; protibiae not at all clavate. Length (of pronotum and elytra): 4.0 mm. Width (at humeri): 2.0 mm.

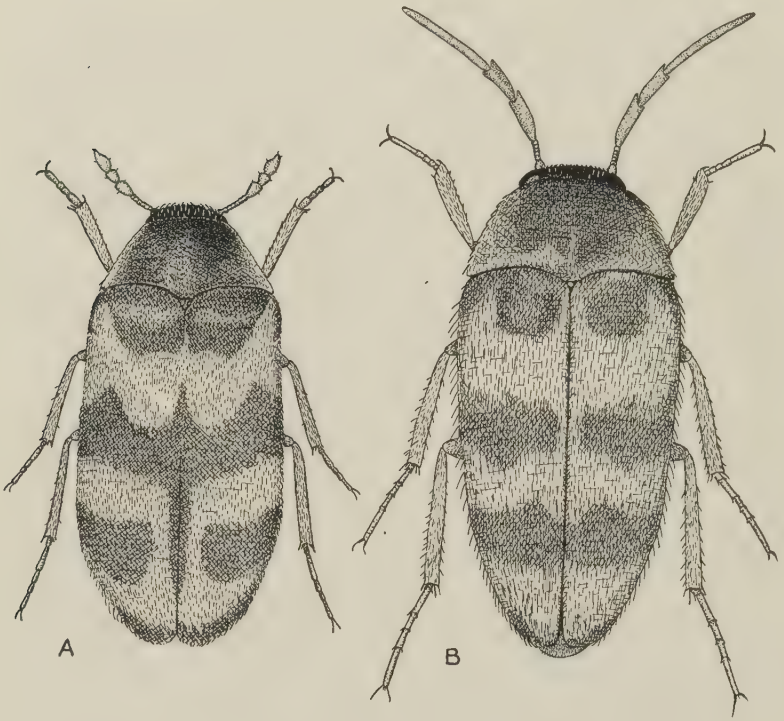
Holotype, male (deposited in collection of the U. S. National Museum): Beaver Canyon, Idaho, July 23 (Hubbard and Schwarz).

This species is quite distinct from all others discussed in this paper. It differs not only in its unicolorous pubescence and integument, but in the longer, finer character of the pubescence, in the absence of short spines on the dorsal margins of the tibiae, and in the lateral extension of the metacoxae to the metepimera. While it is known at present only from the single male listed above, it is quite possible that there are other specimens assembled in collections along with unidentified species of *Attagenus*, which it superficially resembles.

Novelsis picta Casey (Figs. 1B, 3.)

Novelsis picta Casey, 1900, Jour. N. Y. Ent. Soc., 8:148.—Dalla Torre, 1911, Col. Cat., 33:59.

ADULT MALE.—Color of integument of head black; pronotum and elytra light to dark brown; undersurfaces piceous to black with legs and antennae brown to piceous. Pubescence of dorsal surfaces of golden-brown to piceous hairs and white hairs; hairs moderately coarse, recumbent except along lateral margins of elytra where hairs suberect and approximately twice as long as hairs on disc; pattern of pubescence as illustrated; pubescence of ventral surfaces moderately coarse, appressed, white. Antenna ten-segmented; configuration as illustrated; segments of club densely clothed with fine pilosity. Lateral margin dividing hypomeron and pronotum angulate, becoming somewhat carinate posteriad; surface of hypomeron relatively flat. Epipleuron somewhat transversely oblique, terminating gradually and indefinitely beyond hind margin of first abdominal sternite. Metacoxal lamina barely attaining inner margin of metepisternum. Legs moderately



Text-figure 1.—(A) *Novelsis timia* Beal, ♀. (B) *Novelsis picta* Casey, ♂.

stout (profemur less than three and one half times as long as wide); tibiae armed on dorsal side with short spines; protibiae very slightly clavate. Length (of pronotum and elytra) varying from 2.9 mm. to 3.5 mm. Ratio of length to width (across humeri) varying from 1:0.47 to 1:0.49.

Type locality.—Riverside, Arizona. Type specimen in the U. S. National Museum. No other recorded distribution.

New records: ARIZONA: Hot Springs, June 26 (Barber and Schwarz); West of Tucson, June 25, 1927 (E. H. Graham); San Luis, June 16, 1940 (W. F. Barr). CALIFORNIA: Four miles east of Yermo, San Bernardino County, August 27, 1952 (H. B. Leech and J. W. Green).

Novelsis uteana Casey (Figs. 2A, 3.)

Novelsis byturoides Casey, 1900, Jour. N. Y. Ent. Soc., 8:148.—Dalla Torre, 1911, Col. Cat., 33:59 (new synonymy).

Novelsis uteana Casey, 1900, Jour. N. Y. Ent. Soc., 8:148.—Dalla Torre, 1911, Col. Cat., 33:59.

ADULT MALE.—Color of integument of head and pronotum black; integument of elytra brown to dark brown; integument of undersurfaces black with legs and antennae light to dark brown. Pubescence of dorsal surfaces of golden-brown and white hairs; hairs moderately coarse, recumbent except along lateral margins of pronotum and elytra where hairs suberect and two to two and one half times as long as hairs of disc of elytra; pattern of pubescence as illustrated; pubescence of ventral surfaces moderately coarse, appressed, white. Antenna ten-segmented; configuration as illustrated; segments of club densely clothed with fine pilosity. Lateral margin dividing hypomeron and pronotum somewhat rounding or angulate; surface of hypomeron relatively flat. Epipleuron somewhat transversely oblique, terminating gradually and indefinitely. Metacoxal lamina not extending laterad beyond medial third of hind margin of metepisternum. Legs moderately stout; tibiae armed on dorsal side with short spines; protibiae moderately clavate. Length (of pronotum and elytra) varying from 2.3 mm. to 3.0 mm. Ratio of length to width (across humeri) varying from 1 :0.49 to 1 :0.57.

ADULT FEMALE.—Integument of elytra uniformly light brown to uniformly dark brown or dark brown with extremely variable light brown maculae following general pattern of light pubescence of male. Pubescence of dorsal surfaces uniformly white or white intermigled with golden-brown; a pattern of subbasal, diagonal, light band and light, sutural line sometimes visible on elytra in specimens with large proportion of golden-brown hairs; erect hairs along margins of elytra two and one half to three and one half times as long as hairs on disc of elytra. First and second segments of antennal club subequal, each two thirds to three fourths as long as first segment. Length (of pronotum and elytra) varying from 2.6 mm. to 3.7 mm.

Type locality.—Southwestern Utah. Type specimen in the U. S. National Museum. The type locality of *byturoides* is Arizona.

Distribution of specimens examined.—ARIZONA: Blaisdell, June 2, 1919 (E. Schiffel); Bumble Bee, June 13, 1919 (E. Schiffel); Globe (D. K. Duncan); Phoenix (Liebeck collection; Chas. Palm); Santa Rita Mountains, June 8, 1937 (D. J. and J. N. Knull); Tempe (Liebeck collection); Tucson, May 6, 1947 (R. S. Beal); Yuma, May 3, 5, 1918 (J. C. Bradley); April 2, 1924 (R. Hopping). CALIFORNIA: Borego, San Diego County, April 24, 1949 (L. W. Quate); Coachella, May 25, 1928 (Van Dyke collection); Furnace Creek, Death Valley, April 8, 1939 (E. G. Linsley); Holtville (V. L. Wildermuth); Independence, Inyo County, June 10-15, 1929 (E. P. VanDuzee); June 11, 19 (R. L. Usinger); June 1, 1905 (A. Fenyes collection); Indio (A. Fenyes); Lone Pine, Inyo County, June 6, 1937 (N. W. Frazier); June 15, 1913 (R. Hopping collection); Palm Springs, April (A. Fenyes collection); North end of Salton Sea, May 25, 1940; Yermo, June 9, 1940 (W. F. Barr); Yuma, April 22, 1904 (A. Fenyes collection). NEVADA: Glendale, May 25, 1935 (Van Dyke collection); Overton, June 17, 1935 (G. F. Knowlton). NEW MEXICO: Hidalgo County,

May 17, 1946 (D. J. and J. N. Knull). TEXAS: Terlingua, Brewster County, May 6, 1927 (J. O. Martin). UTAH: St. George, May 28, 1935 (Van Dyke collection). LOWER CALIFORNIA: El Mayor, April, 1939 (C. D. Michener); 40 miles west of Mexicali, May, 1939 (C. D. Michener); 20 miles west of Mexicali, May, 1939 (C. D. Michener); 12 miles south of Palacio, May, 1939 (C. D. Michener).

Some confusion has surrounded the taxonomic status of this species. No doubt responsible for this is the degree of sexual dimorphism found in the species, a degree unusual in the Dermestidae. Jayne evidently included the species with his *hornii,* since both are found under that name in the material which he studied (the Horn collection in the Academy of Natural Sciences of Philadelphia). To his description of *hornii* Jayne added the comment that "the female is byturodes Cr." However, Crotch's use of the name was in manuscript only. Since Jayne added a description and figure of the female, the name would seem to be fixed as his. Subsequently Casey separated the two species involved and described as new the species *byturoides.* This name must, accordingly, be considered a homonym. In the same paper Casey described the female of the species under the name *uteana.* This is the only available name for the species and the one by which it should be designated.

In the females are to be found evidences of geographic variation which are not so readily discernible in the males. Females from the Santa Rita Mountains and from Tucson, Arizona, have a nearly equal number of white and golden-brown hairs on the elytra, while females from the more westerly parts of the range of the species are clothed entirely with white hairs. It may be that two subspecies are involved here, but the data and characters observed at present do not seem to warrant a separation of the forms.

The number of segments in the antenna of *uteana* immediately separate it from all species with a similar elytral pattern except for females of *andersoni.* The females of these two species, however, are readily separated by the clearly marked elytral pattern of *andersoni* and the quite indistinct or non-existent elytral pattern of *uteana.*

Novelsis horni (Jayne)

Attagenus Hornii Jayne, 1882, Proc. Amer. Philo. Soc., 20:356, figs. 18, 19, 24, 25.—Sharp, 1902, Biol. Centr.-Amer., Col., 2(1):645.
Attagenus byturodes Jayne, 1882, Proc. Amer. Philo. Soc. 20:356.
Novelsis horni, Casey, 1900, Jour. N. Y. Ent. Soc., 8:148.—Rees, 1943, U. S. D. A. Misc. Pub., 511:15, fig. 2.—Beal, 1951, Pan. Pac. Ent., 27:57.

Adult Male.—Color of integument of dorsal surfaces dark brown to black with light yellowish-brown maculae on pronotum and elytra; pronotum light-maculate on basal margin with occasional, vague, light spots near antero-lateral angles; elytra with light-maculate sutural line extending from base to apex and narrow, transverse or somewhat oblique band at basal fourth; transverse band expanded at lateral margin, but not extended posteriad beyond basal two-fifths; integument of undersurfaces dark brown to black with legs and antennae light to dark brown. Pubescence of dorsal surfaces of black and light golden-brown or whitish hairs; pubescence of pronotum variable, but usually with mostly dark hairs on disc; light pubescence of elytra mostly confined to areas of light maculation; hairs moderately coarse, subrecumbent; hairs along margins of elytra one and one half to two times as long as hairs of disc, scarcely visible from above; pubescence of ventral surfaces white, moderately coarse, appressed. Antenna eleven-segmented; ratios of lengths of first, second, and third segments of antennal club approximately 11:11:18; segments of club densely clothed with fine pilosity. Lateral margin dividing hypomeron and pronotum somewhat angulate but not carinate; surface of hypomeron relatively flat. Epipleuron somewhat transversely oblique, terminating about middle of first abdominal sternite. Metacoxal lamina extending laterad barely as far as inner margin of metepisternum. Legs moderately slender; tibiae armed on dorsal side with short spines; protibiae only slightly clavate. Length (of pronotum and elytra) varying from 2.4 mm. to 2.9 mm. Ratio of length (of pronotum and elytra) to width (across humeri) varying from 1:0.42 to 1:0.50.

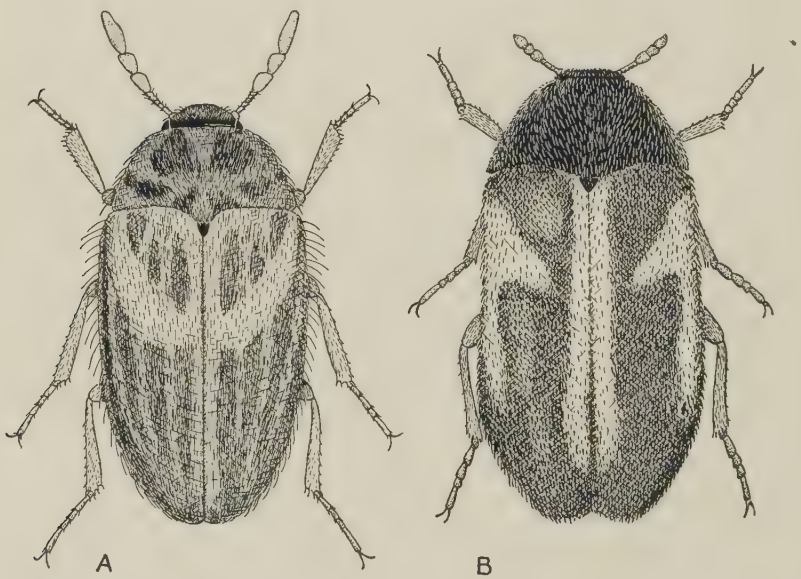
Adult Female.—Second segment of antennal club about one sixth shorter than first; third segment of club about one third longer than first. Length (of pronotum and elytra) varying from 2.8 mm. to 4.0 mm.

Type locality.—Western States. Lectotype in the Academy of Natural Sciences of Philadephia.

Distribution of specimens examined.—Arizona: Catalina Springs, Santa Catalina Mountains, April 10 (Hubbard and Schwarz); Steam Pump, Santa Catalina Mountains, May, 1912 (J. R. Slevin); Douglas, January 25, 1935 (W. W. Jones); Globe, May 17, 1925 (D. K. Duncan); Nogales, April 8, 1940, April 21, 1950; Tucson, March 22, 1948 (R. S. Beal), April 29 (Hubbard and Schwarz). California: Porterville, April 15, 1948 (W. B. Richardson); San Francisco, April 23, 1942 (Van Dyke), May 23, 1919 (J. I. Carlson). New Mexico: Santa Fe (Boyle; Cockerell); Jemez

Mountains, May 20, June 17, July 13 (Jno. Woodgate); Mesilla Park, May 17, 1904 (C. N. Ainslie); Las Cruces. TEXAS: Fort Bliss, May 1, 1915 (J. I. Carlson); Cotulla, March 27, 1908 (Jones and Pratt); North Braunfels, June 27; Sabinal, April, 1910 (F. C. Pratt); San Diego, March 25, 1908 (Jones and Pratt). LOUISIANA: Wills Point (Moyer).

The species also occurs at undetermined localities in Mexico, having been intercepted at border agriculture inspection stations at Laredo, Texas, and Nogales, Arizona. Sharp records *Attagenus horni* from Mexico City and from Frontera in Tabasco. Unquestionably the species does not normally occur around San Francisco. One of the two specimens recorded from there was taken on a box of insects from Arizona, and both it and the other specimen were doubtlessly introduced. It is highly questionable whether the species normally occurs in the vicinity of Porterville, California.



Text-figure 2. (A) *Novelsis uteana* Casey, ♂. (B) *Novelsis andersoni* Beal, ♀.

Novelsis andersoni new species [1] (Fig. 2B.)

ADULT MALE.—Color of integument of head and pronotum entirely black; elytra piceous-black with light yellowish-brown maculae; undersurfaces black with legs and antennae light brown. Pubescence of head and pronotum predominantly of white hairs with a very few scattered piceous hairs; pubescence of elytra of white and piceous hairs with white hairs mostly limited to areas of light maculation; pattern of pubescence similar to that of illustration; hairs moderately coarse, subrecumbent; hairs along margins of elytra one and one half times as long as hairs on disc, scarcely visible from above; pubescence of ventral surfaces white, moderately coarse, appressed. Antenna eleven-segmented; first two segments of club one and one third times as long as ultimate segment; segments of club densely clothed with fine pilosity. Lateral margin dividing hypomeron and pronotum angulate but not carinate; surface of hypomeron relatively flat. Epipleuron somewhat transversely oblique, terminating indefinitely at or behind posterior margin of first abdominal sternite. Metacoxal lamina extending laterad barely as far as inner margin of metepisternum. Legs moderately stout; tibiae armed on dorsal side with short spines; protibiae slightly clavate. Length (of pronotum and elytra) : 2.4 mm. Width (across humeri) : 1.1 mm.

ADULT FEMALE.—Antenna ten-segmented; first and second segments of antennal club subequal, each about five sevenths as long as ultimate segment. Length (of pronotum and elytra) : 3.2 mm. Width (across humeri) : 1.5 mm.

Range of observed variations.—Transverse band of light maculation at basal fourth of elytron extending from humerus to sutural line or extending from humerus only half way across elytron, not meeting sutural line of light maculation; lateral line of light maculation sometimes evanescent, but always indicated by line of light pubescence. Ratio of length to width varying from 1 :0.45 to 1 :0.51.

Holotype, male, and allotype, female (deposited in the California Academy of Sciences) : forty miles west of Mexicali, Lower California, April, 1939 (C. D. Michener).

Paratypes: ARIZONA: Phoenix, April 28, 1924 (J. O. Martin) ; same locality (Chas. Palm). CALIFORNIA: Fort Yuma, Imperial County, April 15, 1923 (E. P. Van Duzee). LOWER CALIFORNIA: twenty miles west of Mexicali, April, 1939 (C. D. Michener) ; twenty miles south of Palacio, April, 1939 (C. D. Michener) ; paratypes deposited in the California Academy of Sciences, the American Museum of Natural History, the U. S. National Museum, and the collection of the author.

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[1] Named for Dr. W. H. Anderson, who has given great assistance in the preparation of this paper.

Quite evidently, this species and *horni* are closely related. Because of their resemblance they have not previously been recognized as distinct. However, the two can be separated by any one of several characters. The most obvious points of difference are found in the dorsal maculation. The basal margin of the pronotum is always light-maculate in *horni* but black in *andersoni*. Posteriad to the light maculate humerus of the elytron of *andersoni* there extends a line of light maculation at least as far as the posterior third of the elytron. In *horni* there is no such line posteriad to the humerus. The females of the species can be separated as well by the number of segments in the antennal club.

Novelsis timia new species (Fig. 1A.)

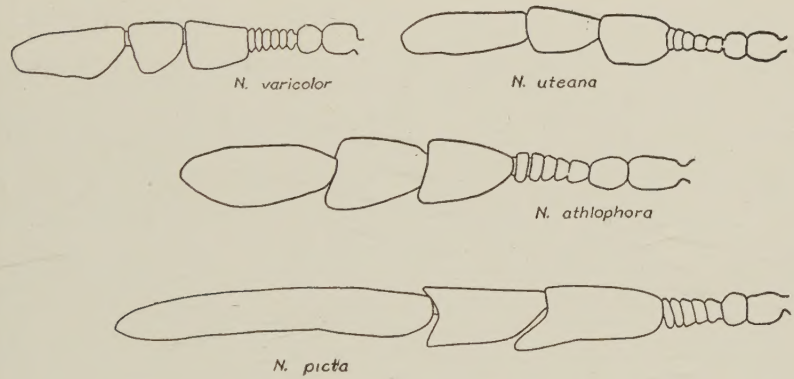
Adult Female.—Color of integument of head piceous; integument of pronotum dark brown becoming lighter brown along lateral and basal margins; integument of elytra brown; integument of undersurfaces piceous with legs and antennae brown. Pubescence of dorsal surfaces of piceous and white hairs; hairs moderately fine, short, recumbent; hairs along margins of elytra one and one half to two times as long as hairs of disc; hairs of head and pronotum almost entirely white; pattern of light and dark hairs of elytra similar to that of illustration; pubescence of ventral surfaces moderately fine, appressed, white. Antenna eleven-segmented; ratios of lengths of first, second, and third segments of antennal club: 5:4:7; segments of club covered with microscopically fine pubescence and a few, scattered, longer hairs. Lateral margin dividing hypomeron and pronotum finely carinate; surface of hypomeron relatively flat. Epipleuron somewhat transversely oblique, terminating gradually well behind hind margin of first abdominal sternite. Metacoxal lamina extending laterad to inner margin of metepisternum. Legs rather slender (profemur four and one tenth times as long as wide); tibiae armed on dorsal side with short spines; protibiae not clavate. Length (of pronotum and elytra): 3.5 mm. Width (across humeri): 1.5 mm.

Variations in paratype: Color of integument of head black; pronotum mottled with black but becoming lighter brown along lateral and basal margins. Pattern of dorsal pubescence as illustrated. Length: 2.9 mm. Width: 1.3 mm.

Holotype, female (deposited in the California Academy of Sciences): Potholes, Imperial County, California, April 9, 1923 (E. P. Van Duzee). One female paratype (deposited in the California Academy of Sciences): Palm Springs, California, May 20, 1905 (A. Fenyes collection).

The character of the pubescence of the antennal club seems to mark these specimens as female. This is a tentative conclusion, since no other sexual characters are visible.

This species is quite distinct from all others in the genus, and is not likely to be confused. Although the elytra bear bands of light pubescence similar to those of *picta*, several characters serve to separate the two. The pronotal pubescence of *timia* is almost entirely white, but in *picta* the pubescence of the disc of the pronotum is predominantly dark. The dorsal pubescence of *timia* is noticeably finer than that of *picta*. The legs of *timia* are more slender than those of *picta*, the differences in proportionate length to width of the profemora being indicated in the accompanying descriptions. The most noticeable difference between the two is in a detail of the elytral patterns. *Timia* has a line of light pubescence connecting the submedian and subapical bands of light pubescence on each elytron. No such line is apparent in *picta*.



Text-figure 3. Male antennae of four species of *Novelsis*.

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